Review Article Compte rendu

Bovine tuberculosis in Canadian wildlife: An updated history

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Abstract — *Mycobacterium bovis* infection in wild animals attracted little attention in Canada until the disease was almost eliminated from domestic livestock. Tuberculosis was endemic in plains bison and occurred in elk, moose, and mule deer in Buffalo National Park (BNP), Alberta during the 1920s and 1930s. Bison were moved from BNP to Wood Buffalo National Park (WBNP), where tuberculosis became, and remains, endemic in bison, posing a risk to efforts to restore bison in northern Canada. Tuberculosis was found in a white-tailed deer in Ontario in 1959, and in an infected elk near Riding Mountain National Park (RMNP), Manitoba in 1992. Intense surveillance has resulted in detection of 40 elk, 8 white-tailed deer, and 7 cattle herds infected between 1997 and 2008 in the RMNP area. The strains of *M. bovis* in the RMNP area are different from strains tested from cattle and bison elsewhere in Canada. Management of tuberculosis in cattle and wild animals is challenging because of uncertainty about the ecology of the disease in various species, difficulty in obtaining samples and population data from wildlife, lack of validated tests, overlapping jurisdictions and authority, and conflicting values and opinions among stakeholders.

Résumé — Tuberculose bovine dans la faune canadienne : Historique mis à jour. L'infection par *Mycobacterium bovis* chez la faune a attiré peu d'attention au Canada jusqu'à ce que la maladie soit presque éliminée du bétail domestique. La tuberculose était endémique chez les bisons des plaines et se présentait chez les wapitis, les orignaux et les cerfs-mulets dans le Parc national Buffalo (PNB), en Alberta, durant les années 1920 et 1930. Les bisons se sont déplacés du PNB jusqu'au Parc national Wood Buffalo (PNWB), où la tuberculose est devenue et demeurée endémique chez les bisons, présentant ainsi un risque pour les efforts de rétablissement des bisons dans le Nord du Canada. La tuberculose a été trouvée chez un cerf de Virginie en Ontario en 1959 et chez un wapiti infecté près du Parc national du Mont-Riding (PNMR), au Manitoba, en 1992. Une surveillance intense a permis le dépistage de 40 wapitis, de 8 cerfs de Virginie et de 7 troupeaux de bétail infectés entre 1997 et 2008 dans la région du PNMR. Les souches de *M. bovis* dans la région du PNMR sont différentes des souches testées chez le bétail et les bisons ailleurs au Canada. La gestion de la tuberculose chez le bétail et la faune est difficile en raison de l'incertitude à propos de l'écologie de la maladie chez les diverses espèces, de la difficulté d'obtenir des échantillons et des données sur la population de la faune, de l'absence de tests validés, du chevauchement des compétences et des autorités ainsi que des valeurs et des opinions conflictuelles parmi les intervenants.

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Introduction

Mycobacterium bovis infection is a chronic debilitating zoonotic disease of cattle. Infection has been identified wherever cattle are raised and eradication of the disease has been attempted in many countries at great cost over many years. Combinations of tuberculin testing to detect infected animals, slaughterhouse monitoring, movement control, and destruction of exposed animals generally have been successful in eliminating the disease, except where a reservoir of infection exists outside the cattle population. Eradication of the disease in livestock has been impeded in several countries by the presence of tuberculosis in wild species. It is believed that in most instances infection originally crossed from livestock to wildlife (1). Although tuberculosis has been reported in a wide range

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of mammals (2), only a few wild species have been identified as maintenance hosts, i.e., hosts in which infection persists through intraspecies transmission in the absence of an external source of *M. bovis.* These include the Eurasian badger *(Meles meles)* in Ireland and the United Kingdom (3); the brush-tailed possum *(Trichosurus vulpecula)* in New Zealand (4); African buffalo *(Syncerus caffer)*, lechwe *(Kobus lechwe)*, warthog *(Phacocoerus africanus)* and kudu *(Tragelaphus strepsiceros)* in Africa (5); white-tailed deer *(Odocoileus virginianus)* in Michigan (6); and red deer *(Cervus elaphus)* and European wild boar *(Sus scrofa)* in Spain (7,8). Other species are thought to be spillover hosts in which tuberculosis does not persist indefinitely without introductions from other species. In some situations, tuberculosis has become an important disease for wild species, either because of its direct effect (4), or because of the impact of control measures on the species.

Efforts to control bovine tuberculosis in cattle began in Canada in 1896 (9) and by 2005 it had been eliminated from cattle herds except for a small area of Manitoba. When Tessaro (10) reviewed tuberculosis in Canadian wildlife in 1986, bison in and around Wood Buffalo National Park (WBNP) were "*the only existing wildlife reservoir*" of *M. bovis* in Canada and the only other occurrences in wild animals had been in a white-tailed deer *(Odocoileus virginianus)* in 1959 (11) and 2 wolves *(Canis lupus)* in 1978 (12).

Tuberculosis in bison

The first recognition of tuberculosis in wild animals in Canada was in bison, and the story of tuberculosis and bison is a fascinating combination of apparent conservation triumphs and serious disease blunders. In the discussion that follows, reference will be made to plains and wood bison, which are generally considered to be subspecies (*B.b. bison* and *B. b. athabascae,* respectively). Although the subspecific designation for wood bison is controversial, genetic distances among sampled bison populations are generally larger between than within the 2 subspecies (13).

Free-ranging plains bison were eliminated from the Canadian prairies in the 1870s and 1880s. Many current herds of plains bison trace to 4 calves captured near Milk River, Alberta in 1873 and taken to Montana (14). In 1885, the herd descended from these calves was purchased by 2 ranchers, Charles Allard and Michel Pablo, who added bison from another source that included stock tracing back to Texas and Saskatchewan. The Allard share of the herd became the foundation for most bison herds in the USA. In 1906, the Canadian government purchased Pablo's share of the herd and, between 1907 and 1912, 716 bison were brought to Canada. The first 410 were released in Elk Island National Park (EINP) in 1907, because facilities were not complete at Buffalo Park Reserve at Wainwright, Alberta (Figure 1). [Buffalo Park Reserve became Buffalo National Park (BNP) in 1913; the latter name will be used here]. In 1909, 325 bison from EINP were delivered and released in BNP. About 48 animals that remained in EINP were the origin of the plains bison herd present there today. [Tuberculosis has not been diagnosed in progeny of the bison that remained at EINP, although approximately 7200 were examined at slaughter between 1928 and 1972 (15) and there has been extensive testing over many years]. Subsequently more bison from Montana were delivered to BNP, for a total of 631 animals. Bison from other sources had been added to the herd at BNP prior to 1914, mostly from a herd in Rocky Mountains Park (later to become Banff National Park) (16–18), and a few from a private herd in Montana that originated from the Allard herd (19). The area of BNP was originally about 411 km^2 and was later increased to 518 km^2 (19), with an estimated carrying capacity of 5000–7000 animals. Buffalo National Park was managed like a "*domestic cattle operation*" and hay was fed during winter (18). The population grew so rapidly that by 1916 newspapers boasted of the largest bison herd in the world (18). In 1923, when 6780 animals were counted, it was decided to slaughter surplus animals (17).

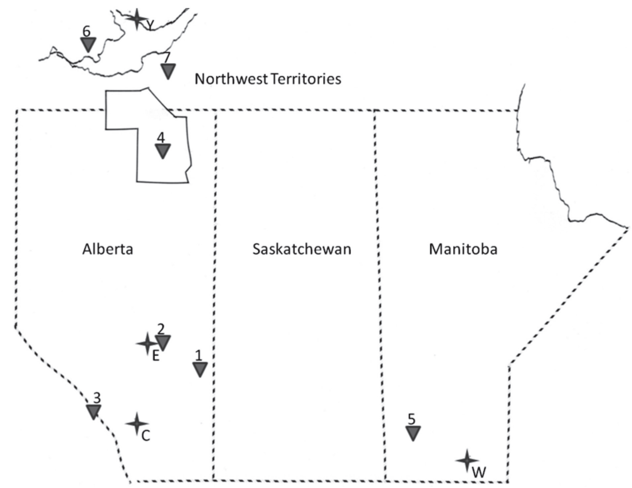

Figure 1. Schematic map of important locations in the history of bovine tuberculosis in wild animals in western Canada. Triangles: 1 – Buffalo National Park 2 – Elk Island National Park, 3 – Banff National Park, 4 – Wood Buffalo National Park, 5 – Riding Mountain National Park, 6 – Mackenzie Bison Sanctuary, 7 – Hook Lake. Stars (for reference): E – Edmonton, C – Calgary, W – Winnipeg, Y – Yellowknife.

Although "*there was apparently no outward indication of tuberculosis*" until 1923 (17), Parks Branch reports described the first case of tuberculosis in 1916 (20). The Deputy Minister of Agriculture was asked for advice, which included segregation of all animals in poor condition from the herd (20). Three additional cases were diagnosed by 1920 (16,21). The Veterinary Director General was notified of the occurrence of tuberculosis in 1919 and offered to supply "*experienced officers*" to conduct the tuberculin test, if "*the Department decided to have this done, and will go to the expense of constructing suitable corrals, chutes, and squeezes*" (20). In 1923, 264 bison were slaughtered and inspected by a dominion veterinary inspector. About 75% of these animals had "*some form of tuberculosis lesion*" (19) and 23% of carcasses were condemned (18). [The animals selected for slaughter included many old bulls and, hence, likely were not representative of the population (16)]. The following winter 1847 bison were slaughtered; all carcasses were inspected, and meat unfit for food was destroyed. "*The presence of disease was withheld from public knowledge as a matter of departmental policy,* and "*it was believed that no more hazard existed than would be the case in the normal slaughter of cattle*" (19). To put this in perspective, 6.4% of cattle killed in Canadian abattoirs in 1922 had tubercular lesions and 1.2% of carcasses were condemned (18), and mandatory whole-herd testing for cattle was begun in 1923 (22). After reviewing the 1923 cull, Dr. F. Torrance, Veterinary Director General, voiced the opinion that the BNP herd was so severely affected that efforts at eradication would be hopeless (18). Veterinarians involved in the slaughter were actively discouraged from reporting tuberculosis in the herd in scientific literature (18), although other less important lesions were described (23).

There were several potential sources for tuberculosis in BNP bison. It might have come with founding animals from Montana. Hadwen (17) considered this unlikely, because animals from that herd, which had remained in EINP, and their descendents have been free of tuberculosis. Officials in the Department of Agriculture believed that the bison were exposed to tuberculosis in Montana when pastured with cattle, and cattle/bison hybrids were present among animals brought from the Pablo herd (18). Infection may have been transferred with bison from what is now Banff National Park to BNP. The Banff herd was established from a variety of sources, including bison from Texas and bison descended from wild calves captured in 1873 and 1874 in Saskatchewan and "*raised to maturity with the assistance of a domestic cow*" (19). In addition, a few cattle/bison hybrids were present in Banff from 1903–1911 (18). Hadwen (17) believed animals from Banff to be the most probable source of infection. In a letter to Parks Commissioner Harkin in 1912, Maxwell Graham, Director of Animals in the Dominion Parks Branch, described the death of 5 bison from tuberculosis "*in our Parks*" in 1910 (24). Brower (18) believed the reference was to Banff, but argued that this was an unlikely source of infection for BNP. Domestic animals used in experiments to produce hybrids at BNP were another potential source. In 1916, an area of BNP was separated from the main bison range by a single wire fence, for use for cross-breeding bison with domestic cattle and yaks *(Bos mutas)*. Maxwell Graham warned that bringing cattle into the park would involve "*considerable additional risk*" from infectious disease for the bison (16). Initial hybrids brought to the park were "*tested for tuberculosis*" prior to introduction (18). Other possible sources were cattle adjacent to the park, but this was thought to represent a minor risk as most of the adjoining land was cultivated with few cattle (16), and "*milch*" cows kept within the park. The latter were "*certified to by a veterinary as being absolutely healthy and free from disease*" and were kept remote from the bison (20).

Regardless of the source of infection, the combination of a bison herd at or beyond the carrying capacity of BNP, and a high prevalence of tuberculosis was a problem. Options considered included slaughtering the herd (an action advocated by Dr. Hadwen) (19); annual slaughters to reduce the population; or moving the surplus to another location. There was considerable public criticism of phased slaughters, and total elimination was considered out of the question. The southern part of Wood Buffalo National Park (WBNP), established in 1922 as a sanctuary for wood bison, was chosen as a site for translocation. Dr. F. Torrance, Veterinary Director General, advised that transplantation of infected bison would almost certainly result in infection of the wood bison, but that the risk would be reduced if only young animals up to the age of yearlings were transferred, and if animals that reacted to the caudal fold tuberculin test (25) were eliminated prior to translocation (16). However, any plan to have the animals tuberculin tested was dropped before shipments of bison were made. Lothian (19) could find no record of why this decision was reached but concluded that it reduced the cost of preparing the animals for shipment, and was based on a belief that the disease was confined to older animals, so that movement of 1- or 2-year-old animals would constitute little risk. Despite extremely vigorous national and international opposition, including condemnation in both Science and Nature (16), this, "*one of the most tragic examples of bureaucratic stupidity in all history*" (26), proceeded as the "*fastest and most economical way to reduce pressure*" at BNP (18). While fierce opposition to the translocation came from biologists, strong veterinary opposition is not evident in historical documents. Between 1925 and 1928, 6673 plains bison (4826 yearlings, 1515 2-year-olds and 332 3-year-olds) from BNP were released at WBNP.

An additional 17 013 bison were slaughtered between 1926 and 1939 to keep the population within the capacity of BNP (16). Of the 11 746 animals killed between 1927 and 1939, 53% had gross lesions of tuberculosis (17).

With the outbreak of war in 1939, the Department of National Defense acquired the BNP area for military training, allowing the National Parks Bureau "*to wind up affairs at Wainwright without admitting publicly that the herd is in bad condition*" [from a memorandum from the director quoted by Lothian (19)]. Elk, moose *(Alces alces),* and mule deer *(Odocoileus hemionus)* were enclosed during fencing of BNP (16), and elk, moose, and pronghorns *(Antilocapra americana)* were purchased for release in the park (18). When the bison herd was eliminated in 1939, these species also were slaughtered. About 6% of 1806 elk and 113 moose, and 2 of 242 mule deer (0.8%) had lesions of tuberculosis (19). The actual prevalence of infection in the cervids was likely greater than indicated by gross lesions (24,27) but it is interesting that the prevalence in cervids was an order of magnitude lower than that in bison in this highly contaminated situation.

Approximately 1500 wood bison existed in WBNP when the plains bison were released. As predicted, hybridization occurred between the introduced and resident bison (13) and the northern herd became infected with tuberculosis. (The herd also became infected with brucellosis, the source for which is less clear). The bison population increased to about 12 000 by 1934 (28) and was more or less constant at "*not less than 10 000 or more than 12 500*" in 1949 and 1951 (16). Beginning about 1970, the population declined markedly to approximately 2200 in 1999 (29) and then increased (30). Tubercular lesions were first noted in bison slaughtered for meat during the 1930's (21) and 38% of male and 40% of female bison slaughtered between 1952 and 1956 had tuberculosis, with almost 3/4 of adult males being positive (16). More recently, 49% of 342 bison captured in WBNP between 1997 and 1999 were positive on either the caudal fold test or a fluorescent polarization assay (31), and prevalence increased with age (29). Despite the decline in population that occurred over a 40-year period, the prevalence of tuberculosis had not declined equivalently, leading Joly and Messier (29) to suggest that "*transmission of tuberculosis may be a nonlinear function of density, where a decline in transmission does not occur until very low densities,*" perhaps because of the gregarious nature of bison.

In 1988, an Environmental Assessment Review Panel was "*requested to examine all reasonable courses of action*"… "*to achieve protection of domestic livestock, wild wood bison, and human health through control or elimination of contact with diseased hybrids*" in the WBNP area (32). The panel concluded "*eradication of the existing bison population is the only method of eliminating the risk of transmission of bovine brucellosis and tuberculosis from bison in and around Wood Buffalo National Park to domestic cattle, wood bison, and humans. After considering the alternatives, the Panel recommends that all free-ranging bison now living in Wood Buffalo National Park and surrounding areas be removed and replaced by disease-free bison.*" This met with considerable criticism and was not acted upon. Subsequent actions and discussion have been reviewed (33). There has been no spread to domestic livestock, although this remains a risk, but the greater threat is to adjacent disease-free wild bison herds (22).

There have been 3 attempts to recover disease-free bison from the WBNP area and, thus, salvage genetic diversity representative of wood bison. In 1958, a group of about 200 bison located in a remote northern section of the park (Nyarling River area) were identified as wood bison type (34). In 1963, 77 of these bison were captured, 61 of which were tested for tuberculosis by the caudal fold test. A 4-year-old bull reacted and was found to have advanced disease (35). A group of animals that tested negative for both tuberculosis and brucellosis was retained and retested, at which time all tested negative and the herd was declared "*disease-free*" (35). In August 1963, 18 of these animals were introduced to an area northwest of Great Slave Lake, as the founders of the herd in the Mackenzie Bison Sanctuary (MBS) (36). This herd increased dramatically in size and then stabilized at about 2000 animals (37). Tuberculosis has not been discovered in the herd. No gross lesions indicative of tuberculosis have been found in any of approximately 500 animals examined from MBS, a small proportion of which have been examined by histology, culture and/or serological tests (38; B. Elkin, personal communication 2008).

In 1965, more bison from Nyarling River were trapped and tested for brucellosis and tuberculosis and 23 test-negative animals were moved to EINP. Three additional calves born to "*positive reactor females*" in WBNP were shipped to EINP in 1967 and 1968 (39). The animals were held separate from the existing plains bison herd and tested at 6-month intervals beginning in 1968. Between November 1968 and September 1969, 10 animals that were test negative when moved from WBNP tested positive for tuberculosis and 4 tested positive for brucellosis (39). In 1969, all test positive animals, together with the remaining animals that originated as adults from WBNP, were destroyed. The current wood bison at EINP are descendants of calves born in EINP or 2 calves from WBNP that were bottle raised. Wilson and Strobeck (13) suggest that this population was founded from 11 individuals.

The 3rd attempt was the Hook Lake Wood Bison Recovery Project (HLWBRP). The Hook Lake herd is a small group (200–500) of wood bison, located northeast of WBNP and east of the Slave River, known to be infected with tuberculosis and brucellosis (40). The HLWBRP was planned as a feasibility study to: 1) conserve genetic diversity of the wild herd through capturing bison calves; 2) eliminate tuberculosis and brucellosis from the captured calves; and 3) raise a disease-free herd from these calves. Methods used have been described in detail (40) but, briefly, about 20 calves, estimated to be $<$ 10 days old when captured in each of 1996, 1997, and 1998 (total 62), were transported to an isolation facility for hand-rearing as pairs in isolation, while being treated intensively with antibiotics. All animals were tested twice annually by the caudal fold test, as well as by fluorescent polarization assay in later years. In 1997, 1 animal captured in 1996 reacted to the caudal fold test, and it and its pen-mate were removed. A single microscopic focus containing acid-fast bacilli was detected in a mediastinal lymph node but no mycobacteria were isolated. In March 2005, (9 y after the project began), multiple enlarged lymph nodes were found in a 2.5-year-old male euthanized and necropsied as part of the herd management strategy. Acid-fast bacilli were found in sections and *M. bovis* was isolated (41). Subsequently other animals in the herd were found to be infected and all animals in the HLWBRP were destroyed in 2006.

A white-tailed deer in Ontario

In November 1959, pleuritis was found in a 2.5-year-old male white-tailed deer examined at a game check-station at Gravenhurst, Ontario (11). The animal was among 440 deer examined at the check-station, located at a site where hunters from a large area of central Ontario could be checked. The hunter observed "*beads*" on the pleura while eviscerating the animal and the lesion was confirmed to be granulomatous pleuritis, from which *M. bovis* was recovered. Belli (11) observed that presence of tuberculosis in deer could be important for the campaign to eradicate bovine tuberculosis, and suggested that "*careful examination of deer carcasses for tuberculosis be instituted.*" That did not occur in 1961 and 1962 when the author participated as a student at the same check-station. The infected deer appears to have been regarded as an isolated event and no record was found of any follow-up investigation. To put this case in perspective, the first general tuberculosis test program for cattle was not completed until 1961 (42).

Riding Mountain National Park (RMNP) area

Riding Mountain National Park (RMNP) was established in 1929 on the site of a federal forest reserve in west-central Manitoba that contained one of the largest herds of wild elk in Canada at the time (15). Elk had been the "*most widely distributed of the deer*" when Europeans reached North America (43) but between 1860 and 1920 the species was eliminated, except in inaccessible areas. Elk in the RMNP area "*survived the 19th century destruction… in perhaps as high numbers as any place outside of Wyoming and Yellowstone National Park*" (44). In 1931, 20 bison from BNP were moved to RMNP and held in a 133 ha fenced area (15). As with the translocation of bison from BNP to WBNP, movement of these animals occurred despite knowledge that tuberculosis was endemic in BNP bison. Tuberculosis was diagnosed in 1937 in an adult cow moved to the park and the herd was eventually depopulated in 1945–1946 (45). The bison were replaced with plains bison from EINP, which have been held in a fenced enclosure, and in which no evidence of tuberculosis has been found on repeated testing.

In 1978, 2 wolf pups found dead in RMNP were found to have lymphadenitis involving abdominal lymph nodes, within which acid-fast bacteria were observed and from which *M. bovis* was isolated (12). DNA extracted from paraffin-embedded, formalin-fixed tissue from 1 wolf confirmed the identity of the bacteria as *M. bovis* (46).

During the 1950's and 1960's, when tuberculosis was not uncommon in Canadian cattle, several outbreaks occurred in cattle near RMNP. The last outbreak from that period in Manitoba was recorded in 1981 (42). In 1991, an outbreak involving 5 cattle herds adjacent to RMNP was detected through routine slaughter surveillance (47). In 1992, an elk shot by a hunter near 1 affected farm was found to have tuberculosis. Following discovery of another infected cattle herd in the same area in 1997, an on-going joint federal-provincial wildlife surveillance program was established. Samples from hunter-killed elk, moose, and white-tailed deer, as well as animals found dead from the vicinity of RMNP were examined for lesions compatible with tuberculosis. Tissues from animals with lesions were examined by bacterial culture and/or polymerase chain reaction (PCR). To July 1, 2008, 9/2347 elk (0.38%) from the vicinity of RMNP and 0/592 hunter-killed elk from the nearby Duck Mountains area (DM), 4/2999 white-tailed deer (0.13%) from the RMNP area and 0/1656 from DM, and none of 562 moose from RMNP and 32 from DM have been confirmed positive by culture of *M. bovis* or histology plus PCR (D. Bergeson, personal communication 2008). The apparent prevalence in hunter-killed animals near RMNP is much lower than that in the "*core*" area of tuberculosis in Michigan in which 2.7% of white-tailed deer (264/9767) sampled in a similar manner between 1995 and 2000 were positive (48). In 2001, tuberculosis was discovered in a single herd of cattle that had been investigated because of proximity to a positive hunter-killed elk (47).

A program to study the distribution and movement of wild elk and deer in the RMNP area was begun in 2002. Blood taken when animals were captured for marking was examined for evidence of tuberculosis using a variety of tests. Any animal found to be positive by any test was recaptured, necropsied, and lymph nodes and other organs were cultured or examined by PCR for *M. bovis*. To July 1, 2008, 241 elk and 25 white-tailed deer have been removed, from which *M. bovis* infection has been confirmed by bacterial isolation or PCR in 28 elk and 2 white-tailed deer. In the spring of 2004, 2/226 white-tailed deer collected by shooting adjacent to RMNP had gross lesions that were confirmed to be tuberculous. Three infected male elk have been found as a result of opportunistic surveillance within RMNP, including 1 killed by another bull in 1988, 1 dead apparently of starvation in 2000, and 1 apparently killed by wolves in 2004 (D. Bergeson, personal communication 2008). In 2003, 3 infected cattle herds were found during farm-to-farm testing of all cattle and captive bison herds in the area around RMNP (47). In that year, an area surrounding RMNP was designated as the Riding Mountain Tuberculosis Eradication Area (RMEA) in which permits are required for movement of cattle and captive bison. In 2004, tuberculosis was detected in a cattle herd that had originated near RMNP but had been moved to another area of the province prior to movement controls (22). In May 2008, tuberculosis was identified in a 5-year-old cow during enhanced surveillance in the RMEA.

All infected cattle herds within the RMEA, except 2, have been in municipalities immediately north or south of the western portion of RMNP, and the great majority of infected elk and deer have been associated with the same area. One marked elk that moved from RMNP to DM was subsequently found to have tuberculosis. Of the 40 known infected elk, 22 were male and 18 were female, whereas 6 of 7 infected white-tailed deer were male.

How *M. bovis* reached RMNP is unknown. It may have come from cattle, as the area was heavily grazed prior to establishment of the park and until 1970 (49). Another possibility is that it was introduced by the bison moved to RMNP from BNP in 1931. However, the strain of *M. bovis* found in all species in the RMNP area is different from that in cattle elsewhere in Canada and from a limited number of bison samples from WBNP that have been tested, indicating a different origin (41). Isolates of *M. bovis* from the RMNP area between 1990 and 2003 including 27 from cattle (all herd outbreaks but 1), 16 from elk, and 1 from a white-tailed deer have been examined by spacer oligonucleotide typing (spoligotyping) (50). Two spoligotype profiles were identified; 40 isolates had 1 profile and 4 (all from cattle) had a 2nd profile that differed only by not having a hybridization signal at one oligonucleotide. The 2 spoligotypes are unique among isolates from Canada and have not been isolated elsewhere (50). DNA extracted from fixed tissue of 1 wolf from 1978 had a spoligotype identical to the predominant type isolated from other animals in the RMNP area, indicating that introduction of this strain was not a recent event (46).

Management of tuberculosis in the RMNP and RMEA has included intense surveillance in livestock and wildlife, fencing to prevent elk and deer using hay storage areas, elk and deer population reduction through extended hunting seasons around the park, removal of any animals that test positive during capture and marking procedures, wolf conservation to increase predation, legislation to prevent baiting and feeding of cervids, and prescribed burning to improve elk habitat within the park area.

Tuberculosis in non-ruminants

Bovine tuberculosis has been identified in many non-ruminant species and some, including Eurasian badgers in Ireland and England and brush-tailed possums in New Zealand, are maintenance hosts. Other species including the ferret *(Mustela furo)* in New Zealand (51), and feral pigs/wild boars are likely spillover hosts in most situations but may maintain the infection under other circumstances. For instance, wild pigs were considered spillover hosts in Australia (51) but European wild boars may be maintenance hosts in Spain (8). *Mycobacterium bovis* has been isolated from coyotes *(Canis latrans)*, raccoons *(Procyon lotor)*, red fox *(Vulpes vulpes)*, black bear *(Ursus americanus)*,

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bobcat *(Lynx rufus)* and opossum *(Didelphis virginianus)* in Michigan. The animals likely became infected through feeding on tuberculous deer (52,53). The only documented instance of tuberculosis in a non-ruminant species in Canada was in the 2 wolves from RMNP in 1978 (12). Tessaro (21) found no evidence of tuberculosis in any of 808 wild animals, of a wide variety of species, collected in and around WBNP between 1983 and 1985. Lesions suggestive of tuberculosis were not detected in any of 7 black bears, 14 mink *(Mustela vison)*, 18 raccoons, 34 wolves, 192 coyotes, 12 beaver *(Castor canadensis)*, 14 foxes, 2 lynx *(Lynx canadensis)*, or 60 Richardson's ground squirrels *(Spermophilus richardsonii)* examined in the RMNP area, nor in any of 120 wolves from the DM (D. Bergeson, personal communication, 2008). Lymph nodes of these animals were cultured for *M. bovis* from 82 coyotes collected during 2004–2005 (54), 60 ground squirrels, and 6 wolves. The lack of tuberculosis in coyotes in the RMNP area contrasts with Michigan where *M. bovis* has been found in 4.8 to 30% of coyotes (55). While the sample of most species examined has been small, there is no evidence that a non-ruminant is a maintenance host in Canada.

Discussion

Mycobacterium bovis infection has been reported in 6 free-ranging species in Canada (bison, elk, moose, white-tailed deer, mule deer, wolf). The ability of any species to serve as a maintenance host for *M. bovis* depends upon a combination of animal features (route of infection, location of lesions, route and level of excretion, and minimum infective dose by different routes), population factors, and conditions for transmission; and "*the mere presence of infection in a wild animal population is not, of itself, evidence that this species is a wildlife reservoir*" (51).

Tuberculosis in bison behaves much as it does in cattle, with respiratory transmission being the major route of infection (38). It is clear that tuberculosis can be maintained over extended periods in small numbers of bison, as occurred during the population decline in WBNP and in bison transferred from BNP to RMNP, from WBNP to EINP, and in the HLWBRP. It also is evident that it is difficult to salvage disease-free bison from infected herds. When tuberculosis became uncommon in Canadian cattle, these same difficulties led to use of whole herd depopulation when tuberculosis was confirmed in a cattle herd. That option was proposed but rejected for both BNP (17) and WBNP (32). The greatest risk at present is that tuberculosis (and brucellosis) will spread from the WBNP area to other wild bison herds, thought to be disease-free, creating a greater conservation dilemma and a larger geographic risk to livestock.

It appears that tuberculosis has persisted within elk under conditions present within at least a portion of RMNP. There is no evidence that moose are infected or that wolves act as maintenance hosts. The role of white-tailed deer in the RMNP area is unclear. Experience in Michigan clearly indicates that this species can be a maintenance host, but the population density and environmental circumstances are different between Michigan and Manitoba, and the apparent prevalence near RMNP seems to be an order of magnitude lower than that in Michigan. However, even if deer are a spillover host, they might act as a source of infection for other species during the time infection persists in the population. Interspecific transmission among elk, deer, and livestock in the RMNP area is likely a very rare event, and how this occurs is unknown.

An unusual feature in the history of bovine tuberculosis is the paucity of recorded tuberculosis in wild cervids at the time when it was common in cattle. The few early cases of tuberculosis in wild cervids in North America were regarded as spillover from cattle, with little likelihood that wild animals would become a reservoir if the disease was eliminated from cattle (56). Three factors may have contributed to the lack of recognition of tuberculosis in cervids in the past, namely that wild cervids were much less abundant than at present, there was little disease surveillance in wildlife, and lesions in cervids may not have been recognized as tuberculosis.

Three phases have been recognized in wild ungulate populations in North America: a pre-European settlement phase, an exploitation phase that extended into the 20th century, and the present. White-tailed deer illustrate this history (57). Prior to European settlement, white-tailed deer were not present in much of their current range in Canada, and density in core range was estimated at about 2–4/km^2. Deer were extirpated from areas and almost totally eliminated during the exploitation phase when the North American population was estimated to be $\leq$ 500 000. The present phase, characterized by reduced or eliminated predators, protective legislation, good habitat conditions, and burgeoning deer populations, began at different times in various locations. The change was dramatic, e.g., Michigan had about 45 000 deer in 1914 and 2 000 000 in 1989 (58). Density in the core area of the tuberculosis outbreak in Michigan deer was about 19–23 deer/km^2 as a result of light harvest of females and supplementary feeding (48).

Because there was little surveillance of wild animals in the past, tuberculosis at low prevalence, as is usual in wild deer, was unlikely to be detected. This has been the case in other countries. For instance, tuberculosis was unknown in wild deer in Ireland until 3.8% of the first samples of hunter-killed animals tested were found to be infected (59). *Mycobacterium bovis* was present in RMNP as early as 1978 (46), but was not detected in a cervid until 1992 and it was only after intense surveillance began in 1997 that the extent of infection became apparent. It is unlikely that any of the 8 infected white-tailed deer found near RMNP would have been detected without the surveillance program. With the benefit of hindsight, the tuberculous deer detected in 1959 near Gravenhurst, Ontario (11) deserved more attention at the time. That deer was remarkably similar to a hunter-killed deer with similar lesions found in Michigan in 1975 (6). In both instances, the deer was believed to be an isolated case and no further surveillance was done. When a second tuberculous deer was found in Michigan in 1994, 13 km from where the 1975 deer was killed, surveillance of deer killed by hunters was initiated. In the first year, 3.5% of deer tested from the area were culture positive for *M. bovis* (6). Spillover of tuberculosis from cattle to deer is estimated to have occurred about 40 y before the problem was recognized in Michigan (60).

The few cases of tuberculosis reported in early years were of advanced disease (6,11,61,62), but lesions in cervids are often inconspicuous (63), confined to cranial lymph nodes, and suppurative rather than caseous or mineralized (64–67). O'Brien (68) stressed "*the necessity of routine and consistent bilateral examination of the cranial nodes*" for diagnosis of tuberculosis in deer, which is unlikely except during a specific surveillance program.

Discussion of management methods that might be used to deal with tuberculosis in Canadian wildlife is beyond the scope of this paper. Lees (47) and Nishi et al (33) have discussed strategies that might be employed. Management of tuberculosis involving livestock and wild animals is inherently much more difficult than when only livestock are involved for many reasons, including that: 1) the range of species that might be involved in transmission, and the ecology of infection in these species, are poorly understood; 2) the distribution, movement, and numbers of wild animals can not be determined easily or with high accuracy; 3) it is difficult to obtain adequate samples from wild populations to define disease at low prevalence; 4) the cost to capture wild animals for in vivo testing is prohibitive and generally impractical, so that postmortem sampling is used and the resulting samples often are not ideal; 5) diagnostic tests have seldom been validated for wild species; 6) legislation that provides the authority for elimination of tuberculosis in livestock may not be applicable to wild animals; 7) there are multiple stakeholders with different objectives, responsibilities, and views of the need for management. While there may be general support for the principle of tuberculosis eradication, there may be less support for specific methods (69); and 8) it is inherently difficult to reduce populations of many wild species, or to maintain them at low density, without using methods that have low public acceptance. Management of disease may involve risks to biodiversity and ecological integrity that are unacceptable to large segments of society.

Tuberculosis is a chronic insidious disease that can remain in an animal for many years. For the disease to persist in a population, infected individuals need, on average, to infect only 1 susceptible individual during their lifetime. It appears that tuberculosis can persist within bison populations at very low density. The nature of the relationship between population size and density, and persistence of tuberculosis in species such as elk and deer are unknown. Long-held assumptions that bovine tuberculosis would not become established in wild cervids have proven wrong. Recent experience in Minnesota, where tuberculosis has been recognized in white-tailed deer at a density of about 2.2/km^2 (calculated from data in reference 70), may require even further rethinking of the density of animals required for disease maintenance. White-tailed deer in North America currently "*exist at higher densities than they have in the past several hundred years*" (71) and other potential reservoirs including feral swine/European wild boars are increasingly present in areas of Canada (72). The problem of tuberculosis in wild species is not unique to Canada, and "*it must be seriously asked whether in future* M. bovis *will be endemic in a gradually changing spectrum of wildlife hosts in different parts of the world*" (73). It is important that surveillance of wild animals be a consideration whenever *M. bovis* infection is identified in any species.

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